

NESTS AND ENEMIES OF *EXOMALOPSIS (PHANAMALOPSIS) SOLANI*
COCKERELL (HYMENOPTERA: APOIDEA, MUTILLIDAE;
DIPTERA: ASILIDAE)

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Abstract.—The bee, *Exomalopsis (Phanomalopsis) solani* Cockerell was studied in Apache, Arizona, 1988 and in Rodeo, New Mexico, 1991. Bees nested communally in hard packed, horizontal ground surrounded by low xeric vegetation. Nest structure, provisions, and larvae are discussed. Evidence of cooperative nesting without differentiation into castes is examined. Cleptoparasites of immatures, *Pseudomethoca bethae* Krombein (Mutillidae) and *Nomada gutierreziae* Cockerell (Apoidea), and a predator of adult bees, *Mallophorina pulchra* Pritchard (Asilidae), are identified.

Key Words: Communal, cleptoparasite, ground-nesting, *Exomalopsis*, Apoidea, Asilidae, Mutillidae

The genus *Exomalopsis* includes primarily small, neotropical bees. *Exomalopsis (Phanomalopsis) solani* Cockerell ranges from Colorado into southern Mexico (Hurd 1979), and is common in southern New Mexico and Arizona (Timberlake 1980). Although it is an abundant species in the American southwest, few nests have been examined (Rozen 1984), and some aspects of the communal nesting behavior of this species require clarification.

MATERIALS AND METHODS

Study sites.—Nest data were obtained by the excavation of three active nests. One nest was examined 30–31 August 1988 by BBN at Apache, Cochise Co., Arizona (Fig. 1). Two nests were excavated 5 and 10 September 1991 by Bryan N. Danforth (pers. comm.) at 2.5 km N of Rodeo, Hidalgo Co., New Mexico. All nests were located in horizontal ground and were surrounded by a diversity of low xeric vegetation, including

Eriogonum, *Euphorbia*, *Gutierrezia*, *Heterotheca*, *Lepidium*, *Mentzelia*, *Solanum*, and *Sphaeralcea*. The soil was hard packed, and consisted of coarse pebbles in a fine, grayish clay/sand matrix.

Nest architecture.—The three nests were completely excavated from the surrounding substrate after blowing fine dry plaster of Paris powder into the opening and tunnels to outline their paths. Soil particles were carefully removed with a small paintbrush, penknife, tablespoon, and shovel. Additional soil was removed in a 10 cm radius surrounding the traced burrows, in an effort to locate plugged laterals and additional cells.

Provisions and immatures.—Females were observed while collecting pollen in the field. Scopal pollen on hind legs and pollen in cells were freeze-dried, then mounted on stubs for scanning electron microscope observation and photographing. Immatures, ranging from first instar to post-defecating larvae, were collected and preserved in

Kahle's solution for microscopic examination.

Communal behavior.—While excavating the 1988 nest at Apache, Arizona, all *E. solani* found within this nest or returning to it with pollen were captured. Only female adults were found, and 19 of the total 21 females were placed in Kahle's solution for later dissection and laboratory examination. Behavior and numbers of females associated with all three nests were observed and recorded. Laboratory analysis, following Batra 1966, included measuring relative body sizes estimated by maximum head width in micrometer units (1 mm = 6.4 units), mandibular wear (estimated by bluntness of mandible tips), wing wear (indicated by the number of nicks in both forewings), ovarian and Dufour's gland development (micrometer units), and gut contents (empty, nectar, pollen).

Enemies.—All insects found within the bee nests or in the area near them were collected and identified. Immature stages, removed from bee cells, were placed in shallow wells in a covered plastic culture dish and returned to the laboratory for rearing. Voucher specimens of all insects collected during this study were deposited in the National Museum of Natural History, Smithsonian Institution.

RESULTS AND DISCUSSION

Nest architecture.—The inconspicuous nest entrances were smooth, circular openings into the horizontal soil surface. They were 4.5 mm in diameter, and devoid of a surrounding turret or tumulus. Each nest consisted of a main tunnel that descended perpendicularly from the ground surface with twists and minor detours around rocks. The cells were encountered at depths ranging from about 30–50 cm. Cells appeared to be arranged in horizontal linear series that radiated from the main vertical shaft. The lateral tunnels containing these cells were filled with loose soil, and cells were



Fig. 1. Excavation of *Exomalopsis solani* Cockerell nest, Apache, Arizona, 31 August 1988.

always separated by a distance of 1 cm or more. Because of the difficulty in tracing these soil-filled laterals, and their close proximity to one another, it was not possible to determine the exact number of cells per lateral. Cell bases were always lower than cell caps, but cell orientation relative to the lateral was highly variable. Table 1 provides data from the three nests. The presence of many old, previously used cells in two of the nests suggests that natal nests are reused by subsequent generations. Perhaps this explains the earlier observation (Linsley et al. 1954) that *E. solani* appropriates abandoned burrows. Previously used cells were easily identified by a thin layer of fungal hyphae covering the cell walls (Fig. 2F).

Cell walls were harder than the surrounding soil, and cells could be extracted without breaking. Walls of empty new cells did not test positive for glucose, so it is assumed

Table 1. Comparison of three *Exomalopsis solani* nests.

	Nest #1 30-31 Aug. 1988	Nest #2 5 Sept. 1991	Nest #3 10 Sept. 1991
Adult females present	19	6	1
Maximum nest depth	51 cm	40 cm	44 cm
Total cells	44	35	43
Cells with eggs	5	11	3
Cells with larvae	20	17	13
Incomplete cells	5	4	1
Moldy cells	6	3	25
Parasitized cells	8	0	2

that water, rather than nectar was used during excavation. Cell measurements ranged from 8.0–9.5 mm in length and 5.0–5.5 mm in width ($n = 25$). Cells were lined internally with a delicate, transparent, somewhat glossy, hydrophobic material (Fig. 2D) probably secreted by the Dufour's gland. Cell caps were 3.8–4.2 mm in diameter ($n = 15$) and consisted of 4–5 concentric coils (Fig. 2A). These closures consisted of rough, appressed soil pellets and, unlike cell walls, were not waterproof (Fig. 2B, C). Tunnel walls (Fig. 2E) also were unlined, allowing water to pass through quickly, but like cell walls, they had an almost polished appearance when viewed without magnification. They were not as strong as cells, but were somewhat harder than the surrounding soil.

Provisions and immatures.—Cell provisions were oblong pollen and nectar masses with the distal portion conforming to the cell base. Their surfaces were smooth and moist, and a cheesy odor, such as that associated with *Anthophora* (Norden et al. 1980), was not detected. The "ventral foot" as mentioned by Rozen (1984) was not observed. Plant pollens of several species were present in each of the cells examined ($n = 5$) and they appeared to be distributed throughout the masses (Fig. 3A). In one cell, four different pollens were found (Fig. 3B). The other cells each contained mixtures of three pollens. Foraging *E. solani* females ($n = 8$) were observed to collect and carry only

one species of pollen per load (Fig. 3D). This finding may support Michener's (1966) suggestion that individual cells are provisioned by more than one female, or may simply reflect changes in pollen availability over the course of time. Completed pollen masses were coated with a material that appeared to provide anti-fungal benefits (Fig. 3C). Hyphae readily invaded, however, when incomplete masses were abandoned, or they were broken open, exposing internal provision contents (Fig. 3E, F).

Placement of a single egg was atop the pollen mass or towards one side, as described by Rozen (1984). Feeding larvae encircled their provisions as they grew. They resembled larvae of *E. chionura* Cockerell (Rozen 1957). Fecal pellets were spread throughout the cell, but were never on cell caps. No larvae spun cocoons.

Communal behavior.—Michener (1966) noted that multiple nest occupancy occurs regularly in the genus *Exomalopsis*. Upon first approaching the Apache, Arizona nest, a single female was positioned in the opening with her head level with the ground. When a blade of grass was poked into the hole, she retreated into the tunnel, turned, then positioned herself abdomen up, effectively plugging the entrance. Scraping the ground surface surrounding the nest opening in preparation for digging caused the guarding female to again retreat deeper into her nest. Nineteen of the 21 females occupying this nest were preserved and analyzed to determine their probable roles within the group nest.

The size of females varied little. Head width ranged from 16.0–17.5 units, with an average of 16.5 units. Mandibular wear also varied little, and the tips of all mandibles were blunted, indicating that all females may have participated in nest excavation. Wing wear however, varied considerably, ranging from 5 to 22 nicks per bee ($\bar{x} = 12.78$). Similarly, ovarian development was also quite variable. The largest oocyte per bee ranged from 6–21 micrometer units ($\bar{x} =$

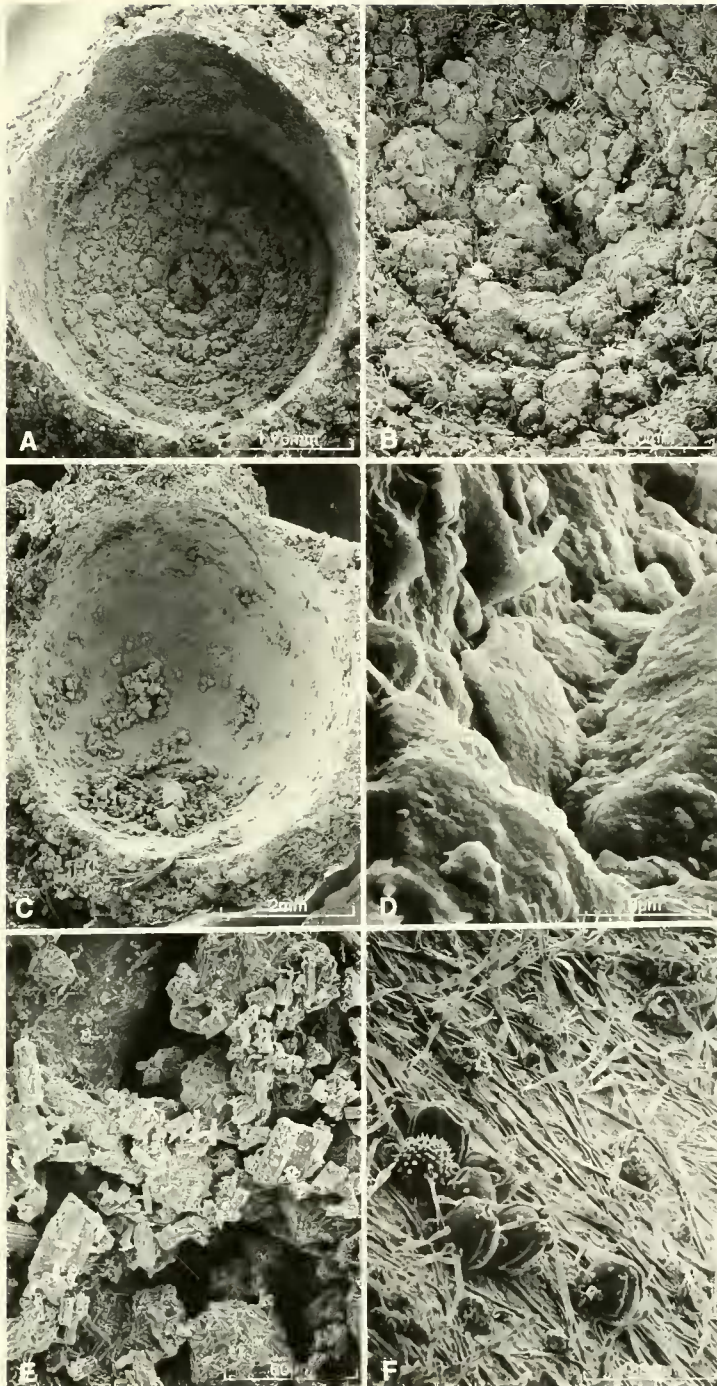


Fig. 2. Scanning electron micrographs of *Exomalopsis solani* nest structures. A, interior view of cell closure showing the concentric coils. B, magnified cap showing uncoated soil pellets composing the coils. C, view into cell base showing smooth interior and rough texture of surrounding soil that has fallen in. D, cell lining coating soil particles of the cell interior surface. E, closeup of tunnel walls revealing no lining material. F, portion of interior wall of a used cell showing several uneaten pollen grains and fungal mycelium covering the cell lining.

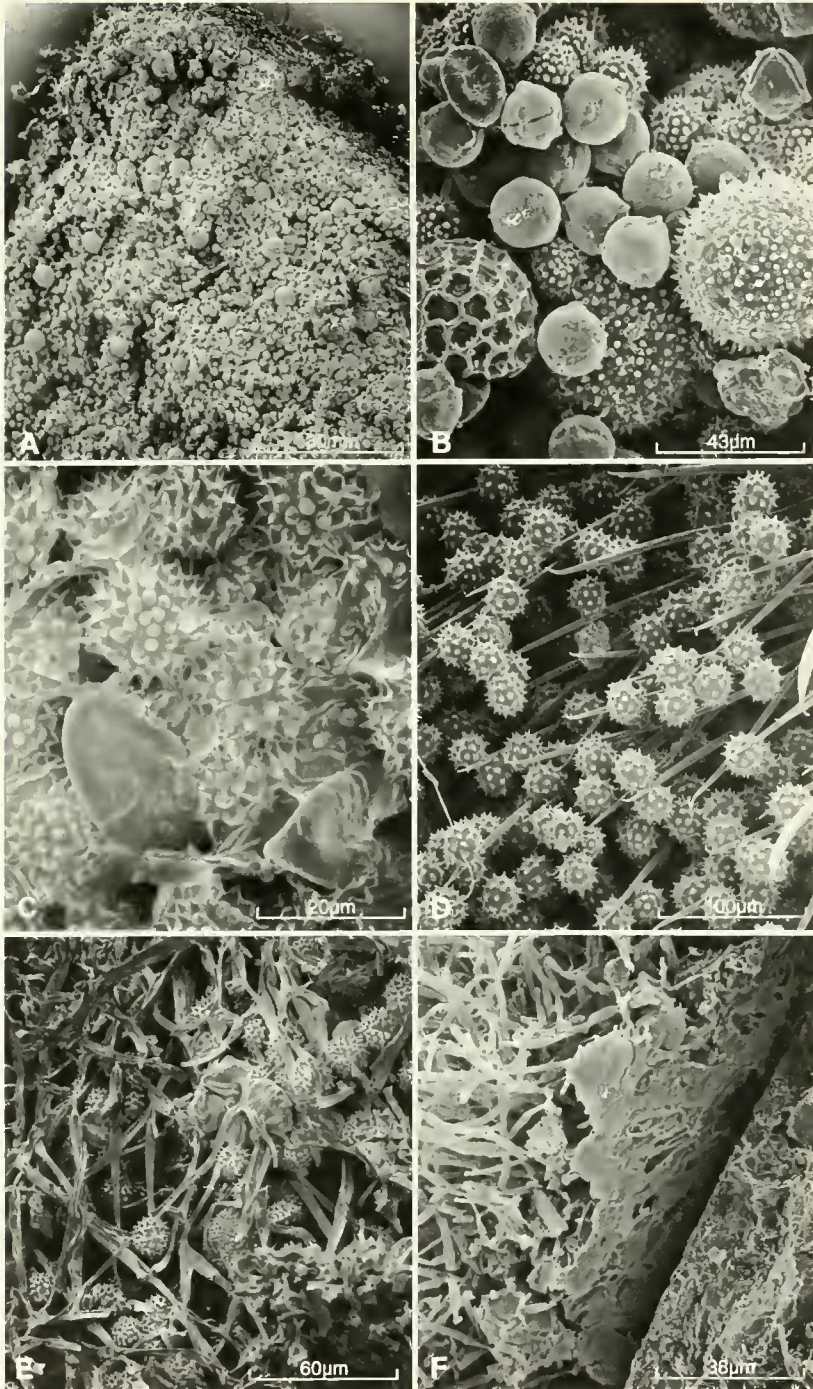


Fig. 3. Scanning electron micrographs of *Exomalopsis solani* provisions. A, pollen mass revealing distribution of different pollens throughout. B, one mass with at least four different pollens present. C, surface of completed pollen mass showing coating that may have an anti-fungal effect. D, scopa of foraging female *E. solani* with pollen collected from only one host plant. E, fungal hyphae invading a pollen mass that had been cut in half with a sterile scalpel. F, incomplete pollen mass with fungal hyphae filling the cell and pulling the lining from the cell's earthen wall.

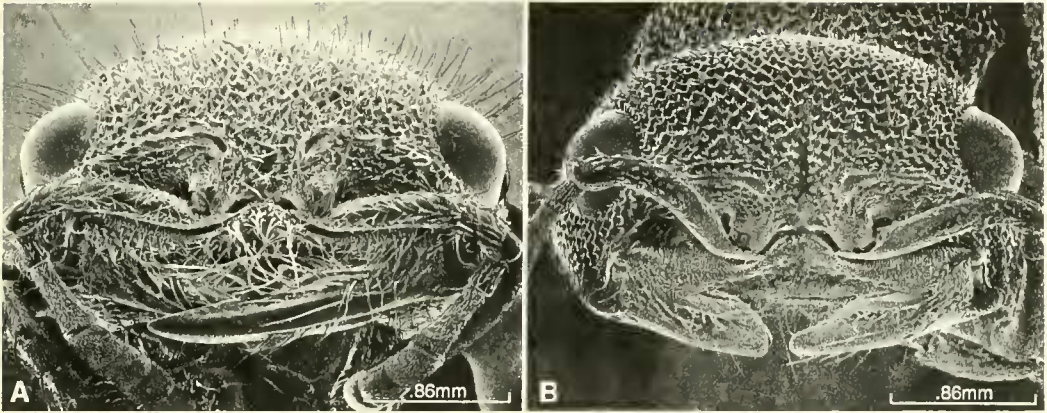


Fig. 4. Frontal view of heads of cleptoparasitic wasp, *Pseudomethocha bethae*. A, pristine female collected on ground near *E. solani* nest. B, female showing considerable mandibular wear that was collected within *E. solani* nest.

12.47 units). Eleven of the 13 females that had enlarged ovaries with an egg larger than the mean, had recently eaten nectar and pollen; four of the six females with smaller ovaries had not eaten recently. The size of the Dufour's gland was not well correlated with the size of the ovaries. However, the Dufour's gland of a bee can shrink suddenly whenever its secretion has been applied to a cell.

The two known foragers, captured returning to the nest with pollen, were of average size (16 and 17 units) and had average mandibular wear. One had a large oocyte (16 units), but the other had small oocytes (6 units). The wings of both bees were very worn (20 and 21 nicks). The three bees that had the largest oocytes (21, 16, and 16 units) were of average size (16, 16, and 17 units). They had 20, 11, and 10 wing nicks respectively, somewhat above average wing wear. Their mandibular wear was nearly average. These data indicate that, although this species nests communally, and shares a single nest entrance, there is no evident differentiation into workers and egglayers. Unfortunately, there was not time to mark individual bees and watch them to determine which individuals were foragers, and during what time in their lives. Our data support Michener's (1966) finding that *E.*

solani nests cooperatively, without the development of castes.

Enemies.—Two adult female mutillids, *Pseudomethocha bethae* Krombein (1992), were found within the Apache nest during the 1988 excavation. These wasps are known cleptoparasites of bee larvae. One individual with somewhat eroded mandibles was on a cell provision, presumably feeding; the other, with badly eroded mandibles (Fig. 4B), was within the main tunnel 39 cm below ground. We assume that mandibular wear occurred as the wasps chewed into the hardened brood cells in order to gain access to bee larvae. Nine additional adult females of *P. bethae* (Fig. 4A) were collected crawling on the ground near the Apache and Rodeo nest sites. Also found within one of the Rodeo nests were two cells containing a post-defecating larva and a cocoon of unidentified mutillids (Bryan N. Danforth, pers. comm.).

Another aculeate cleptoparasite found within the Apache nest and in the immediate vicinity was the cuckoo bee, *Nomada gutierreziae* Cockerell. Two *Nomada* larvae were removed from cells containing post-defecating *E. solani* larvae and were preserved. Five female and one male *Nomada* removed from six otherwise empty *E. solani* cells were reared in the laboratory. Co-

coons were not spun by the *Nomada* larvae. Parker (1984) reported this same nomadine [as *Hypochrotaenia* (*Micronomada*) *gutierreziae*] to be a cleptoparasite of the gregariously nesting *Exomalopsis* (*Anthophorula*) *crenulata* Timberlake in southern Utah. Several specimens of another nomadine bee, *Paranomada nitida* Linsley, were collected by KVK near the Apache nest. While not directly associated with *E. solani*, *P. nitida* is highly suspect since *Paranomada velutina* Linsley was recorded in the nests by Rozen (1984). *Triopasites penniger* (Cockerell), also collected by KVK near the Apache nest, has been associated with *Exomalopsis* (Jerome G. Rozen, Jr., pers. comm.).

The only observed predator of adult *E. solani* was the asilid fly, *Mallophorina pulchra* Pritchard. Flies perched on flower stems throughout the Apache and Rodeo nesting areas and grabbed bees as they foraged. Other insects comparable in size to *E. solani* were also taken as prey by the asilid, although flies of this genus are reported to specialize in the collection of Hymenoptera (Cole and Pritchard 1964).

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